BREVIORA

Museum of Comparative Zoology

Cambridge, Mass. July 10, 1963 Number 187

THE LABYRINTHODONT DENTITION[1]

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Because of the phylogenetic importance of the Labyrinthodontia, numerous studies have been made of the cranial anatomy of members of this great amphibian group. Little, however, has been written regarding their dentition. My attention was called to this subject because of the unusual nature of the dentition of a newly discovered trimerorhachoid rhachitome from the Texas Permian, which is to be described in a forthcoming paper as *Neldasaurus wrightae*.[2] In the present paper I shall review our current knowledge of the dentition of the Labyrinthodontia as a whole. The data on which this review is based, summarized in Table 1, were drawn directly from specimens in a few instances but most were obtained from the literature; measurements recorded are those quoted by authors or determined from scale drawings of original or reconstructed specimens. Fifty-one genera, including temnospondyls, anthracosaurs and a crossopterygian were reviewed. The arrangement of labyrinthodont genera in the table is essentially as in Romer's 1947 classification (pp. 310-319).

Characteristic of labyrinthodonts generally is a dentition which includes, in addition to marginal tooth rows, palatal tusks and often, at least, a shagreen of denticles on the palate and the coronoid region of the lower jaw. The primitive condition, it would seem, was one in which a relatively small number of marginal teeth were present and the palatal dentition consisted

[1] This paper is part of a thesis submitted to the Department of Biology of Harvard University as partial fulfillment of the requirements for the degree of Doctor of Philosophy, August, 1962.

[2] This is a *nomen nudum* here, and will enter scientific nomenclature with the publication of my projected description of this new form.

of a single stout tusk-pair on each of the three lateral palatal elements. There is, however, wide variation in the number of marginal teeth, and in various instances a trend toward reduction in size and concomitant increase in numbers of palatal tusks.

In this paper I have confined attention to the dentition of the upper jaw and palate, since, apart from the occasional presence of symphysial tusks, the lower dentition in great measure mirrors the marginal dentition of the upper jaw. Further, no attempt is made to ascertain how widely a shagreen of tiny denticles is present on the palate, since, even if present, such a shagreen is often destroyed in preparation and consequently unrecorded.

The data presented in the tabulation include:

(1) A formula representing the palatal dentition, recorded in terms of the numbers of tusks (or tusk pits) and small teeth on the vomer, the palatine and the ectopterygoid of one side. For example, the formula for the palatal dentition of *Lyrocephalus* is 2 — 2(3) — (13), which means there are two tusks on the vomer, two tusks and three smaller teeth on the palatine, and thirteen small teeth on the ectopterygoid.

(2) Information concerning the marginal upper jaw dentition such as (a) the number of premaxillary and maxillary teeth, (b) the presence of regionally enlarged teeth forming "canine peaks" whenever it could be determined, indicated on the table by a plus sign.

(3) Skull length taken as the distance from the tip of the snout to the end of the occipital condyle. (This, taken together with the figure on the number of teeth, will give an indication of relative tooth spacing.)

(4) Sources, placed here to avoid repetition in the text.

It is generally and reasonably assumed that labyrinthodonts are descended from rhipidistian crossopterygians. The dentition is known in only a few crossopterygians, such as *Eusthenopteron, Megalichthys* and *Ectosteorhachis*. In *Eusthenopteron* of the Upper Devonian we find: (1) a series of very numerous small marginal teeth, (2) a row of numerous small teeth along the outer margins of the vomer, palatine and ectopterygoid, (3) larger tusks, few in number, placed more medially on these three elements, with some indication of tusk and pit pairing; as far as known the vomer bears only one pair of tusks.

In the following discussion we will consider marginal and palatal dentitions separately.

MARGINAL TEETH

The oldest known labyrinthodont, *Ichthyostega* from East Greenland beds near the Devonian-Carboniferous boundary, is somewhat off the main line of labyrinthodont evolution but shows a modest number of well spaced teeth — 8-9 premaxillary, 16-18 maxillary — of fairly good size, most about the same length but with the posterior premaxillary teeth somewhat enlarged. *Acanthostega*, an ichthyostegalian of comparable age, appears to have had more maxillary teeth — about 30. Romer (1947) provisionally associated the Colosteidae of Linton with the ichthyostegals. The marginal dentition of the colosteid *Erpetosaurus*, however, does not agree with that of the ichthyostegals, for here, in contrast, there is a reduced number of rather large premaxillary teeth and very numerous small maxillary teeth.

All further well-known labyrinthodonts can be clearly divided into temnospondyls and anthracosaurs. The marginal dentition of temnospondyls will be dealt with first.

The most primitive temnospondyls (apart from their peculiar "keyhole orbit") are clearly the loxommids, such as *Baphetes* and *Megalocephalus*. In the number of premaxillary teeth both appear primitive, but the maxillary series — 21 in *Baphetes*, 40 in *Megalocephalus* — are in contrast, the larger number being perhaps proportional to skull elongation in *Megalocephalus*.

Exemplifying the next higher stage are the edopsoids, *Edops* and *Eugyrinus* (the last was considered a trimerorhachoid by Romer, but recent studies by Carroll indicate that *Eugyrinus* is more primitive and generalized than the trimerorhachoids). Here the premaxillary teeth are primitive in number (9, ?7) and the number of maxillary teeth (24, 29) is fairly low.

Among trimerorhachoids, some agree fairly well with the primitive edopsoid pattern (the maxillary count of 19 in *Saurerpeton* is lower) but within the group there is a notable tendency toward an increase in the number of marginal teeth. The premaxillary count increases from 9 in *Saurerpeton* to 12 in *Trimerorhachis* and *Eobrachyops* and to 15 in *Neldasaurus* and *Drinosaurus*. The number of maxillary teeth is somewhat increased in *Eobrachyops*, *Drinosaurus* and *Trimerorhachis* and increased to the spectacularly high number of approximately 93 in *Neldasaurus*.

Certain forms which Romer grouped as the Micropholoidea show characters more or less intermediate between primitive edopsoids and the "typical" rhachitomes of the Lower Permian.

Three members of the group — *Archegosaurus*, *Chenoprosopus* and *Lysipterygium* — show a "normal" rhachitomous tooth count with 8-11 premaxillary and 27-29 maxillary teeth; *Micropholis*, however, has a reduced dentition with 5 premaxillary and 16 maxillary teeth, while *Platyops*, in correlation with an extremely elongate skull, has a total of about 65 marginal teeth in the upper jaw.

The "typical" rhachitomes, the Eryopsoidea, include a wide variety of Permian labyrinthodonts and a few Carboniferous predecessors. Dental formulas are given for nine members of this group (nos. 20-28, Table 1) and show some variation within the group. Premaxillary teeth range from a maximum of 15 in the broad-snouted *Zatrachys* and its Carboniferous relative *Acanthostoma*, through 13 in *Eryops* to a low figure of 5-8 for *Actinodon*, *Cacops* and trematopsids. Some eryopsoids have a reduced maxillary count with a low of 12 in *Cacops; Eryops*, on the other hand, has an increased count of 38.

The trematosaurs, a persistently rhachitomous, early Triassic, fish-eating group, reflect accompanying snout elongation in tooth numbers. Although the premaxillary teeth retain a count of 10-12, in the long-snouted forms the number of maxillary teeth increases, reaching a figure of 50 in *Trematosuchus*.

The neorhachitomes of the late Permian are presumed to have been derived from eryopsoids. Such a typical form as *Rhinesuchus* has a marginal dentition almost exactly like that of its morphological ancestor *Eryops; Lydekkerina*, however, has a reduced formula, with only 20 maxillary teeth. Still more advanced neorhachitomes of the early Triassic, those apparently leading to the capitosaurs, are such forms as *Wetlugasaurus*, *Volgasaurus* and *Benthosuchus*. Here, facial elongation is accompanied by an increase in the number of maxillary teeth to 52, 56 and 61 in these genera, respectively. A high number of maxillary teeth occurs in capitosaurs, reaching a peak in *Mastodonsaurus*, which has 23 premaxillary and about 75 maxillary teeth. Parallel in development to the capitosaurs are those forms grouped as the metoposaurs. *Metoposaurus* itself has a "generalized" count of 10 premaxillary and 34 maxillary teeth, but in the American species *Eupelor browni* and the European *Eupelor fraasi* the count increases to about 60 maxillary teeth in the former and to 90 in the latter. Certain short-faced Triassic forms tend to have reduced counts; the brachyopid *Batrachosuchus* having but 17 maxillary teeth and the plagiosaur *Gerrothorax* having somewhat over 26.

A group by group account of variations of marginal tooth count in temnospondyls has been presented above. As can be seen, no consistent pattern emerges. One gains the general impression of a probable early temnospondyl condition of 9 or so premaxillary teeth and a maxillary count in the 20's, with a modest increase, on the average, in typical rhachitomes. Occasionally there are reductions to lower figures (as, for example, in *Sclerocephalus, Actinodon,* or the dissorophid *Cacops*). On the whole, however, variations are toward higher figures in later forms. In some cases increases in tooth count are definitely associated either with notable snout elongation, as in *Platyops* and the trematosaurs, or, as in capitosaurs and metoposaurs, with a combination of moderate skull elongation and absolute increase in size, the teeth failing to increase in proportion to the total size of the animal. Most exceptional of all are the trimerorhachoids, particularly *Neldasaurus*, where an exceedingly high tooth count may be found in a skull of modest proportions. No consistent correlation between tooth number and skull size can be demonstrated.

Anthracosaurian dentition is known in only a few, mainly Carboniferous forms. Here the premaxillary teeth are low in number, related to the usually narrow snout and the fairly large size of the individual teeth. Marginal teeth are essentially of two types: either large and few in number, as in *Anthracosaurus* and *Pteroplax*, or small and more numerous, as in *Pholiderpeton, Neopteroplax* and, especially, *Archeria*, where the exact count is indeterminate although the teeth are certainly very numerous. Marginal tooth counts in the premaxilla and maxilla of *Seymouria* are low; *Kotlassia* shows a slight increase over the primitive number.

Regionally enlarged teeth forming "canine peaks" occur sporadically in different labyrinthodont groups but appear to have been fairly common in primitive forms.

PALATAL TEETH

Known rhipidistian crossopterygians have, as mentioned above, (1) a very large number of small teeth in a row along the margins of the vomer, the palatine and the ectopterygoid, (2) larger tusks more medially placed on these three bones. As is well known, in all typical labyrinthodonts the larger teeth are retained while the lateral row of smaller teeth is lost. But, surprisingly, in *Ichthyostega* there is no trace at all of the "tusk" row;

instead it appears that the lateral row of numerous, essentially even-sized teeth has been retained. In this regard *Ichthyostega* is very far removed from the condition expected in the ancestor of later labyrinthodonts.

Primitive temnospondyls proper almost always have one pair of tusks on each of the three bones, the vomer, palatine and ectopterygoid. This is true almost without exception in loxommids, edopsoids and most eryopsoids. Occasionally, a replacement pit may be absent (? or indeterminate) but exceptions are rare. In palatal dentition, colosteids (e.g. *Erpetosaurus*) are typically temnospondyl in character, thus arguing strongly against Romer's suggestion of ichthyostegal relationships for these animals.

In numerous more specialized or advanced labyrinthodonts there is an increase in the number of smaller palatal teeth and a tendency toward reduction of the more prominent tusks, usually those on the ectopterygoid. The presence of this pattern in different groups indicates that this trend has occurred several times in parallel fashion. It is, for example, seen in trimerorhachoids (except *Eobrachyops*), micropholoids and trematosaurs. In *Rhinesuchus*, which appears closely related to typical eryopsoids, this trend is seen again, leading to conditions in capitosaurs where, as in metoposaurs, the increase in the number of small teeth is very prominent. In some short-faced Triassic forms the increase in smaller palatal teeth is not so pronounced — a condition no doubt correlated with the short palate in these animals.

Distinctive of the anthracosaurs is the absence of vomerine teeth — apparently related to the narrow palatal exposure of the vomers in these forms. In the few palates known, there are generally a pair of large palatine tusks and a modest number of ectopterygoid teeth, the front ones tusk-like. In *Pholidogaster*, with six tusk-like teeth on the ectopterygoid, and in *Anthracosaurus*, where a tusk pair is accompanied by a pair of fairly large teeth, we encounter conditions reminiscent of the crossopterygians, in which the palatine had a row of large teeth.

Seymouriamorphs are unusual among anthracosaurs. *Seymouria*, in contrast to other anthracosaurs, has a pair of vomerine tusks and — in parallel fashion to some temnospondyl groups — has lost the ectopterygoid teeth. *Kotlassia* resembles other anthracosaurs in lacking vomerine teeth but has a close-set row of small teeth on the palatine and ectopterygoid, decreasing gradually in size from front to back. These differences between known anthracosaurians suggest much variation within the group, but the extent of this variation is at present incompletely known.

I wish to express my appreciation to Dr. Alfred S. Romer of the Museum of Comparative Zoology for his generous aid and many helpful suggestions during the preparation of this paper. I am also indebted to Professor Bryan Patterson and Dr. Ernest E. Williams of the Museum of Comparative Zoology for constructive criticism of the manuscript.

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TABLE 1
Labyrinthodont Dentition

Form	Palatal Dentition v - p - ec	Marginal Dentition pmx	Marginal Dentition mx	"Canine Peaks"	Skull Length (in mm.)	Source
1. Eusthenopteron (Crossopterygian)	2 - 3 - 4 (12)-(15)-(28)	20±	60-61		80±	Jarvik (1954)
2. Ichthyostega	(6)-(8-10)-(6)	8-9	16-18	+	150	Jarvik (1952)
3. Erpetosaurus	(2)-2-2	4	49	+	85	Romer (1930; 1947)
						Steen (1931)
4. Baphetes	2 - 2 - 2	8	21	+	270	Watson (1929)
5. Megalocephalus	2 - 2 - 2	7	40	+	330	Watson (1929)
6. Dendrerpeton	0 - 2 - 2	—	—	?	70	Steen (1934)
7. Cochleosaurus	2 - 2 - 2	5?	7?	+	70	Steen (1931; 1938)
8. Edops	2 - 2 - 2	9	24	+	510	Romer and Witter (1942)
9. Eugyrinus	1 - 1 - 0?	7?	29		18	Watson (1940)
10. Saurerpeton	2 - 2 - 2	9	19		60	Romer (1930)
11. Neldasaurus	2-2(8)-2(21)	15	93		158	M.C.Z. 2200
12. Trimerorhachis	2(6)-2(8)-(6)	12	38		100±	Case (1935)
13. Eobrachyops	1 - 2 - 1	12?	30		79	Watson (1956)
14. Dvinosaurus	2(12)-2-1(5)	15	30		180	Sushkin (1936)
						Bystrow (1938)
15. Archegosaurus	4 - 2(4) - (6)	8	27	+	350	Watson (1919)
						Whittard (1928)
16. Chenoprosopus	2 - 2 - 2	11	29	+	224	Langston (1953)
						Romer (1947)
						Watson (1919)

TABLE 1 (Cont.)
Labyrinthodont Dentition

Form	Palatal Dentition v - p - ec	Marginal Dentition pmx	Marginal Dentition mx	"Canine Peaks"	Skull Length (in mm.)	Source
17. Lysipterygium	0 - (9) - (4)	8	29		58	Branson (1935)
18. Platyops	2(15)-2(6)-(22)	—	-65-		278	Efremov (1933)
						Bystrow (1935)
19. Micropholis	2(2) - (3) - 0	5	16		34	Watson (1913)
						Broili, Schroeder (1937)
20. Eryops	2 - 2 - 2	13	38	+	356	Sawin (1941)
21. Sclerocephalus	2 - 2 - 4	10	14		156	Broili (1926)
						Romer (1947)
22. Actinodon	1 - 2 - 2	7	16	+	170	Gaudry (1887)
						Thevenin (1910)
23. Cacops	1 - 2 - 0	8	12		127	Williston (1910)
24. Acheloma	2 - 2 - 2	5	25	+	63	M.C.Z. 1419
25. Trematops	2 - 2 - 2	7	23	+	63	Olson (1941)
						Williston (1909)
26. Parioxys	2 - 2 - 2	6	30	+	142	M.C.Z. 1162
27. Zatrachys	2 - 2 - 2	15	15-17	+	104	Langston (1953)
28. Acanthostoma	2 - 2 - 2	15	34		40	Steen (1937)
29. Lyrocephalus	2-2(3)-(13)	10	32	+	166	Säve-Söderbergh (1936)
30. Trematosuchus	2(10)-1(4)-1(12)	12	50	+	411	Haughton (1915; 1925)
31. Trematosaurus	2(4)-2(2)-(19)	6	40	+	157	Watson (1919)
32. Platystega	2(6)-2(2)-(18)	12	32	+	335	Säve-Söderbergh (1936)
33. Rhinesuchus	2(5)-2(21)-(9)	13	39	+	90	Watson (1919)
						Haughton (1925)

34. Lydekkerina	2(3)-1(5)-0	10	20		76	Watson (1912)
						Broili and Schroeder (1937)
35. Wetlugasaurus	2(14)-2(11)-(14)	15	52		160	Bystrow and Efremov (1940)
36. Volgasaurus	1(18)-2(14)-2(19)	14	56		123	Efremov (1940)
37. Benthosuchus	2(27)-2(10)-(19)	13	61		123	Bystrow (1935)
						Efremov (1940)
38. Mastodonsaurus	2(34)-2(10)-(30)	23	75		666	Fraas (1889)
						Watson (1919)
39. Metoposaurus	2(16)-2(8)-(14)	10	34		294	Watson (1919)
40. Eupelor (Anaschisma)	2(6) 2(9) 0	22	48-60		456	Branson and Mehl (1929)
41. Eupelor (Buettneria)	2(18)-2(9)-(30)	13	90		380	Case (1922)
						Sawin (1945)
42. Batrachosuchus	(7)-1(3)-(4)	12	17		156	Romer (1947)
						Watson (1956)
43. Gerrothorax	(11)-(6)-(5)	8	26±		132	Nilsson (1934, 1937)
44. Pholidogaster	0-2(2)-6		-29-		—	Watson (1929)
45. Anthracosaurus	0-2-2(2)	4	17	+	288	Watson (1929)
46. Anthracosaurus (Linton)	0 - 2 - 2(+?)	3	25±	+		Romer (1963)
47. Pholiderpeton	0 - 2 - 2(3)	3	40	+	240	Watson (1929)
48. Pteroplax	0 - 2 - 2(8)	6	27		400±	Watson (1912, 1926)
						Atthey (1876)
49. Neopteroplax	0 - 2 - 2(4)	3	37	+		Romer (1963)
50. Seymouria	2 - 2 - 0	5	17	+	170	White (1939)
						Williston (1911)
51. Kotlassia	0 - (7)-(10-13)	8-9	29-32		190	Bystrow (1944)